

Macroevolution and the biological diversity of plants and herbivores

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Terrestrial biodiversity is dominated by plants and the herbivores that consume them, and they are one of the major conduits of energy flow up to higher trophic levels. Here, we address the processes that have generated the spectacular diversity of flowering plants (>300,000 species) and insect herbivores (likely >1 million species). Long-standing macroevolutionary hypotheses have postulated that reciprocal evolution of adaptations and subsequent bursts of speciation have given rise to much of this biodiversity. We critically evaluate various predictions based on this coevolutionary theory. Phylogenetic reconstruction of ancestral states has revealed evidence for escalation in the potency or variety of plant lineages' chemical defenses; however, escalation of defense has been moderated by tradeoffs and alternative strategies (e.g., tolerance or defense by biotic agents). There is still surprisingly scant evidence that novel defense traits reduce herbivory and that such evolutionary novelty spurs diversification. Consistent with the coevolutionary hypothesis, there is some evidence that diversification of herbivores has lagged behind, but has nevertheless been temporally correlated with that of their host-plant clades, indicating colonization and radiation of insects on diversifying plants. However, there is still limited support for the role of host-plant shifts in insect diversification. Finally, a frontier area of research, and a general conclusion of our review, is that community ecology and the long-term evolutionary history of plant and insect diversification are inexorably intertwined.

coevolution | herbivory | insect host range | phylogenetic analyses | plant defense theory

One hundred and fifty years ago, Darwin's concept of evolution replaced theological concepts of plenitude as an explanation for the almost boundless diversity of organisms. Since then, evolutionary biologists and ecologists have sought to understand how such diversity has come to be, how it has changed over time, and why species diversity varies among taxa and environments. For the last several decades, plants and their herbivores, especially insects, have been major subjects of such inquiries, for together they account for more than half of the described species and play overwhelmingly important ecological roles.

Central to this topic has been the immense diversity of so-called secondary compounds or secondary metabolites that distinguish species and higher taxa of plants and the relatively narrow host range of most phytophagous insects, most species of which feed on a small fraction of the plants in any area. Secondary compounds are those not involved in the "primary" functions of plants, that is, resource acquisition and allocation, and are often implicated in defense. The suspicion that plant secondary chemistry had shaped specialized host associations (1) was elaborated and verified by Dethier (2) and others, and Fraenkel (3) summarized the evidence that most secondary compounds had evolved to defend plants against insects and other natural enemies. In one of the most frequently cited publications on plant–herbivore interactions, "Butterflies and plants: A study in coevolution," Ehr-

lich and Raven (4) integrated these ideas into a historical scenario that inspired researchers for decades thereafter.

Ehrlich and Raven (4) suggested that in response to herbivory a plant species may evolve a novel, highly effective chemical defense that enables escape from most or all of its associated herbivores. By an unspecified mechanism, this advantage enables the plant lineage to radiate into diverse species, which share the novel defense (hence, related plants tend to share similar chemistry). After some time, one or more insect species colonize this plant clade and adapt to it, shifting from perhaps chemically similar, although distantly related, host plants. These insects, able to use the "empty niches" afforded by a diverse clade of chemically distinctive plants, themselves undergo adaptive radiation, as new species arise and adapt to different, but related, plants. Hence related insects will tend to use related plant hosts, a pattern long known to entomologists and that Ehrlich and Raven described in detail as it is manifested by butterflies. Ehrlich and Raven proposed that repetition of such stepwise adaptive radiations through time, in both plant–herbivore and other kinds of ecological associations, accounts for a great deal of biological diversity (Fig. 1).

However inspiring their article may have been, most research in the next three decades or so did not address the historical, macroevolutionary components that were Ehrlich and Raven's focus (5). Considerable literature addressed the still-debated question of

whether or not the function (not just effect) of secondary compounds is defense, and attention shifted from explanation of the variety of taxonomically restricted compounds to the costs and benefits of varying degrees of investment in defense. For example, Feeny (6) suggested that investment should be greater in "apparent" (large, long-lived, common species) plants than less apparent (rarer, smaller, or more ephemeral) species; Janzen (7) and Coley et al. (8) proposed that allocation to defense would be especially high in plants that have inherently slow growth because of limited resources, a hypothesis for which strong support has been adduced (e.g., ref. 9). This ecological (or microevolutionary) approach, based on assumptions of optimal adaptation, was complemented by studies of selection in populations, especially using methods of quantitative genetics. This body of work has strongly established that secondary compounds are heritable, herbivores do indeed exert selection for defense, and negative genetic correlations often exist that imply tradeoffs in investment (10, 11). An important outcome of these approaches was recognition that plants may adapt to herbivory not only by "resistance" to herbivores (preventing or minimizing attack), but also by "toler-

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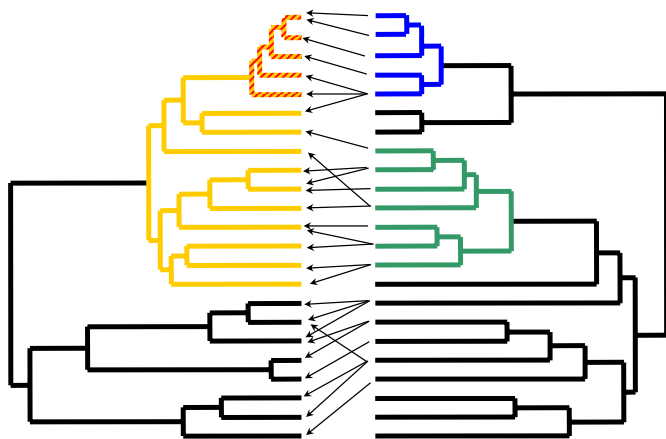


Fig. 1. A conceptualization of escape and radiate coevolution hypothesized by Ehrlich and Raven (4). In this hypothetical scenario, a plant phylogeny is on the left and insect herbivore phylogeny is on the right; arrows between the phylogenies indicate host use (species missing arrows feed on plants that are not shown here). For the plant lineage, black indicates the ancestral defensive phenotype, yellow indicates the evolution of some new defense, and yellow with red hatches indicates the evolution of an additional novel defense. The evolution of counteradaptations is similarly indicated on the insect phylogeny. Note that the evolution of novel traits related to the interaction is associated with an increased diversification rate (i.e., species accumulation per unit time). Insect counteradaptations have allowed for the colonization of differentially defended plant clades, but in this case the counteradaptations have not escalated by adding on new phenotypes; rather, two counteradaptations have independently evolved. Insect host use shows some phylogenetic signal (i.e., closely related species feed on related plants), but some insects also colonize distantly related plants. The insect lineage did not cospeciate with the plant lineage. In other words, the phylogenies are not parallel (i.e., mirror images of each other), but rather the pattern indicates that insects radiated onto existing plants (fossil evidence or other means of dating could verify this pattern of insect speciation on to a diversified group of plants). Parallel phylogenies are not predicted by coevolution, and could simply be a consequence of joint vicariance events that result in both insect and plant speciation.

ance” of tissue damage, based on an ability to regrow or reproduce, by using stored resources (12, 13). Research on phytophagous insects included explorations of sensory and other physiological aspects of choice of and adaptation to host plants (e.g., refs. 14 and 15), studies of host-plant-associated speciation (16–18), and especially quantitative genetic approaches to the question of whether or not tradeoffs exist in adaptation to different host plants. The latter approach is the dominant hypothesis to explain the prevalence of specialized host associations (19, 20).

Research on the historical, macroevolutionary heart of Ehrlich and Raven’s hypothesis (4) was slow in developing, probably because the relevant fossil record is rather sparse (but see ref. 21) and phylogenetic methods were in their infancy (and were embroiled in controversy) in the 1960s. Important steps toward using phylogenies to infer the history of associations were first taken by Mitter and Brooks (22) at a time when phylogenies were few and based on little (nonmolecular) data. Today, phylogenetic analysis, based on ever more sophisticated analytical methods and abundant molecular data, enables us to infer with considerable confidence not only the order of branching, but also approxi-

mate timing and the pattern of evolution of characters of interest.

One consequence of this sea change in evolutionary biology is a growing appreciation of the impact of deep evolutionary history on the features of living organisms, including features that affect their ecological distribution and associations (23–25). As a prelude to the other papers in this Special Feature, we briefly outline some of the major issues in the macroevolution of plant–herbivore interactions (see also ref. 26). Of course, satisfying answers to most of these questions will require integrating macroevolutionary pattern with evidence from functional, genetic, and ecological approaches.

Evolution of Defenses

Herbivory clearly imposes natural selection on plants (e.g., refs. 11 and 27), even enforcing habitat specialization (9), so the defensive function of many plant secondary chemicals is no longer doubted. That does not mean, however, that all secondary compounds have defensive function, and criteria for determining this are still not fully developed. Phylogenies enable use of the comparative method, in which patterns of convergent evolution may provide evidence of adaptation (28). In some cases, suites

of plant features seem to form “defense syndromes” (29, 30) that may indicate adaptation to particular suites of herbivores and may potentially be dictated by the abiotic environment. Many classes of compounds seem to have evolved repeatedly from widely shared biosynthetic pathways, suggesting that fairly minor changes in gene regulation may be entailed (31, 32), and some authors have suggested that many plant compounds may be derived either directly or by lateral gene transfer from symbiotic fungi (32). These suggestions imply that rampant parallelism or convergence is possible, potentially providing plentiful opportunity for phylogenetic comparisons. They also bear on the important question of whether plants’ defense profiles are optimized (as they might be if most lineages retain the same biosynthetic capacities, so that specific families of compounds can readily evolve) or are historically contingent on the occurrence of rare mutations. Does the chemical variation among plant lineages owe more to the origin of phenotypic variation or different histories of selection?

Plant adaptations to herbivory can be classified by several criteria, such as biosynthetic pathway, investment level, and effect on the target organisms. For example, tolerance rather than resistance may be advantageous if resources are relatively abundant (9, 33). Chemical resistance characters may act as toxins, inhibitors of digestion, or deterrents. Whether or not these classes of defense differ in phylogenetic conservatism or the ecological context in which they are most often deployed is not known. One can easily imagine that alteration of many plant features could knock out necessary sign stimuli for oviposition or feeding by certain specialized insects, so that compounds that act as deterrents could be more variable among plant taxa than toxins (34). Evidence that specialist insects are deterred by a great variety of compounds is consonant with this view (14).

Phylogenetic analysis of ancestral and derived states of defense profiles, including specific chemical families, has only begun, yet it can address some of the most important questions about defense evolution. Several of the articles in this Special Feature address the impact of ecological associations on the macroevolution of defense strategies, ranging from biotic defense via ants to investment in sundry chemical classes (35, 36). Plant life history, genetic attributes, and mating system also may play a role in the macroevolution of defense strategies; Johnson et al.’s (37) study of the *Onagraceae* clearly demonstrates that repeated evolution of asexual reproduc-

tion influenced the evolution of defense against herbivores. Phylogenetic reconstruction of ancestral states further allows the dissection of some classic predictions from defense theory. For example, does continuing herbivore pressure, especially if imposed by steadily adapting herbivores, result in “escalation” (38) in the potency or variety of a plant lineage’s chemical defense system? Or does adaptation to herbivory reside mostly in evolving novel defenses? There are clear cases of evolutionary novelty, such as the origin of the sulfur-based glucosinolate-myrosinase defense system in the Brassicaceae. This potent defense is diagnostic for the family; yet restricted genera in the Brassicaceae have additionally evolved novel compound classes [e.g., tropane alkaloids (39), cucurbitacins (40), and cardenolides (41)] that typically occur in other plant families. The evolution of furanocoumarins in Apiaceae is thought to have entailed progression toward more toxic forms (42), but a firm phylogenetic framework has not yet been established. Among milkweeds (*Asclepias* spp.), phenolic compounds and tolerance to herbivory appear to have increased, but the toxic cardenolides for which these plants are renowned have declined during the diversification of the genus (43, 44). In this Special Feature, Becerra et al. (45) report a pattern of escalation in the *Bursera* system, in which the diversity of terpenoid defenses has increased.

A phylogenetic pattern of escalation or the progressive addition of novel defense strategies implicates coevolution consistent with an arms race. Alternatively, a pattern of old defenses being replaced by new ones suggests that energetic cost or other tradeoffs constrain the macroevolution of defense (46). However, this explanation has been questioned because physiological tradeoffs between different kinds of defenses seem not to be general (29, 47). Ecological costs, such as deterring pollinators, have also been described (48, 49). A more intriguing possibility is that like chemical insecticides, defenses become obsolete because herbivores adapt to them. Cornell and Hawkins (50) draw this conclusion from their metaanalysis of experimental studies, in which taxonomically broadly distributed compounds, which Cornell and Hawkins assume to be pleiomorphic, display somewhat lower toxicity than taxonomically restricted (presumably more recently evolved) compounds. This proposition warrants more detailed examination. Ultimately, tradeoffs must constrain investment in

defense. We predict that tradeoffs over macroevolutionary scales will entail tradeoffs in “strategies” (e.g., chemical toxins vs. tolerance) more often than in single compound types (29, 30, 35, 36).

An important question is whether most chemical defenses are effective against a wide or narrow range of actual and potential herbivores. High specificity might imply that a diverse community of insects selects for multiple defenses, as seen in many plants, and could account for divergence in defense profiles among plant species. Thus coevolution (in the sense of reciprocal adaptive responses) would entail “pairwise” evolution of specific plant traits and specific enemies. In this scenario, individual species of herbivores are each abundant and damaging enough to impose significant selection and do not strongly interact over evolutionary time. Alternatively, coevolution would be “diffuse” if defense against various enemies were positively genetically correlated (51, 52); then selection for defense could stem from the collective impact of many herbivores, some of which might be uncommon (34), and the evolution of new defenses would be impelled not by the identity of herbivores as much as by their collective impact. Probably the question of the incidence of pairwise versus diffuse defense evolution will vary with factors such as plant organ (e.g., fruit vs. leaf), defense type, and herbivore diet breadth. Even crude measures of the toxicity or deterrent effects of specific compounds across a wide array of insects appear to be rather rare, and those few suggest that effects are not highly correlated across herbivores (53–55). Genetic correlations of resistance of whole plants against various herbivores are also rather low (56–58), but these correlations, across genotypes that vary in many characters, may say little about the cross-effectiveness of any one defense character.

Finally, what are the macroecological and macroevolutionary consequences of defense evolution? Do evolutionarily new defense profiles result in escape from some herbivores and reduced herbivory, as Ehrlich and Raven (4) postulated? This seems likely, in view of the different taxonomic composition of the insects associated with different plant taxa, but we are aware of few rigorous investigations of this question. Perhaps the best circumstantial evidence comes from the Brassicaceae (discussed above), where the ancestral defenses (glucosinolates) have been overcome by many specialist insects, yet several newer novel defenses (39–41) strongly limit many of the specialists (59). Armbruster et al.

(60) have shown that the phylogenetically derived condition of producing foliar defense resins in the genus *Dalechampia* is deterrent to several generalist and specialist herbivores. Ultimately, we suggest phylogenetic–ecological studies that examine the impact of herbivores on sister groups that differ in defensive traits. Such studies would not only contribute to understanding the impact of novel traits on herbivory, but also on the association of different herbivore communities with different defense strategies (see discussion on diffuse coevolution above).

Ehrlich and Raven (4) also proposed that the advantage provided by new defenses could promote adaptive radiation of a plant lineage. Just why an individually advantageous character might elevate speciation rates is not obvious (see ref. 61), but diversification rates could be enhanced by larger population sizes, which encourage the colonization of marginal habitats, or by reducing the frequency of extinction. Ehrlich and Raven’s hypothesis is best tested by comparing the diversity in multiple lineages, in which a proposed diversity-enhancing character has evolved convergently, with their sister lineages. Using this approach, Farrell et al. (62) reported that diversity is significantly elevated in lineages that have evolved latex- or resin-bearing canals. This appears to be the only such analysis to date. Other highly convergent and more or less discrete traits such as the production of glandular trichomes or alkaloids are ripe for such analyses.

In a quantitative sense, a directional relationship between a continuous character and phylogenetic node depth suggests that the trait impacts diversification (63) (although cause and effect are not separable); such relationships have been detected in the milkweeds (43, 44). A final approach to addressing the role of plant defensive traits in adaptive radiation is to test Simpson’s classic “early burst” prediction, that trait diversity within a lineage should evolve early in the diversification process and plateau toward the end of the radiation (64–66). In this Special Feature, Agrawal et al. (67) provide some of the first phylogenetic evidence for the early burst model, implicating a contribution of plant defenses to the adaptive radiation of the milkweeds (*Asclepias* spp.).

Evolution of Herbivores

Most herbivorous mammals have fairly broad diets, but among insects highly polyphagous species are relatively few, and most species are restricted to plants in a single family or even to a few closely related species (15, 68). The av-

erage herbivorous insect species collected from trees in a highly diverse New Guinea forest feeds on three or fewer plant species and has >90% of individuals concentrated on a single species (69). Moreover, many clades of phytophagous insects are models of phylogenetic conservatism, having largely retained association with the same plant taxa for many millions of years, with few evolutionary excursions to other taxa. In a broad-scale phylogenetic survey, Janz and Nylin (70) report that related butterfly larvae tend to feed on related host plants and host shifts were more common between closely related plants than between distantly related plants. In a more recent compilation of phylogenies of phytophagous insects, Winkler and Mitter (71) found that only $\approx 8\%$ of speciation events included a host shift to a different plant family. In conformity with Ehrlich and Raven's scenario (4), most of the diversification of insect host associations is based on shifts among plant lineages that had evolved earlier, for almost no instances of cospeciation or congruence between plant and insect phylogenies have been described, and molecular dating shows that at least some insect clades are younger than the plant clades with which they are associated (71). For example, the radiation of pierine butterflies (cabbage white and relatives) began ≈ 10 million years after the diversification of the glucosinolate-containing Brassicales (72). There is some evidence, as yet more intriguing than definitive, that the diversification of insect clades is temporally correlated, although time-lagged, with the diversification of their host-plant clades, a point to which we return later (71).

Although chemical similarity of plant taxa is correlated, overall, with their phylogenetic propinquity, the correlation is not perfect. It has therefore been possible to show that host shifts of related insects are more strongly correlated with plant chemistry than plant phylogeny. Examples include shifts between both congeneric (73) and more distantly related plants (74). Although this correspondence is far from perfect (some shifts appear to have been facilitated instead by ecological propinquity of the ancestral and derived host plants) it suggests that adaptation to all available plants is not equiprobable and evolution of host shifts may be guided in part by limitations on genetic variation in insect species that make some shifts more difficult than others. Futuyma et al. (75, 76) could detect genetic variation in feeding responses of four specialized species of *Ophraella* leaf beetles to

some, but not all, of the plant hosts of congeneric beetles, primarily to hosts of closely related species. The genetic basis of host preferences and the interaction between such genetic variation and ecological processes possibly leading to speciation have recently been studied in several other groups (77–80). More studies of the relationship between the genetic processes and the historical pattern of host shifts are needed, especially in a comparative framework.

The prevalence of phylogenetic conservatism in diet might suggest that specialized host associations are irreversible or nearly so. However, although change from one specialized host association to another is the prevalent pattern, the few well-controlled studies of the phylogeny of host range indicate that specialists give rise to generalists as often as generalists give rise to specialists. Indeed, the frequency of the direction of shifts between these two states may be predictable simply from the proportions of specialist and generalist species: shifts in either direction may be phylogenetically “random” (71, 81). In nymphaline butterflies, the phylogenetic distribution of generalist and specialist species and the frequent parallel origins of specialization on the same few plant lineages led Janz and Nylin (82) to suggest the “oscillation hypothesis.” They posit that specialists retain a physiological ability to use ancestral hosts and that expansion of diet to include such ancestral hosts can serve as an evolutionary bridge to new specialized associations. There is some evidence that “major” host shifts, to different plant families, occur especially in insect lineages that include polyphagous species (71).

What accounts for the great diversity of phytophagous insects? In a now classic article, Mitter et al. (83) showed that herbivorous clades are significantly more species-rich than their plesiomorphically nonherbivorous sister clades: the herbivorous habit appears to have promoted diversification. Many authors have postulated that adaptation to different host plants may cause speciation, i.e., contribute to the evolution of reproductive isolation. Although much of this argument has centered on the question of sympatric speciation (16), “ecological speciation” stemming from divergent ecological selection need not be sympatric (84, 85). There is evidence for both allopatric and sympatric ecological speciation in phytophagous insects (17, 86). Yet, among 145 pairs of presumptive sister species in 45 phylogenies, Winkler and Mitter (71) found divergence in host association in only 48%. They noted that there need be no causal relationship between host use and specia-

tion in many of these cases, and approximately half of speciation events do not entail shift between plant species. For example, in the diversification of 14 *Asphondylia* gall midges on creosote bush (*Larrea tridentata*), shifts to different plant tissues represent adaptive diversification within a single host plant (87). Other attributes, such as an internal versus external feeding habit, may contribute to insect diversification; Nyman et al. (88) reported that in the sawfly subfamily Nematinae feeding habit was more conserved than host use and external feeders host-shifted more than internal feeders, but that feeding habit was not consistently associated with the rate of diversification. Winkler and Mitter (71) conclude that although speciation may be promoted by divergent host use in some cases, the great diversity of phytophagous insects may be attributed to the sheer diversity of ecological niches (in terms of chemistry, structure, organs, etc) afforded by the great diversity of plants.

A key hypothesis in Ehrlich and Raven's coevolution scenario (4) was that insect lineages that adapt to diverse, chemically distinct plant clades should undergo adaptive radiation and enhanced diversification. There is surprisingly little evidence on this point. Even the simple question, whether or not the species diversity of insect clades is correlated with that of their host-plant clades, has been addressed by only a few authors. Basal lineages of Lepidoptera and the beetle clade Phytophaga tend to feed on conifers and are far less diverse than their sister clades, which feed mostly on angiosperms (89, 90). In the most detailed such analysis, Janz et al. (91) found that species diversity of host plants consistently contributes to species diversity of clades of the large butterfly family Nymphalinae. They suggest that increasing host diversity may contribute to speciation by enabling geographic expansion and therefore opportunity for spatial isolation and genetic divergence. Still less do we know whether adaptation to chemically distinct plants fosters adaptive radiation. In perhaps the most convincing example, Wheat et al. (72) ascribe the radiation of the butterfly subfamily Pierinae, which is much more diverse than its sister group, to the evolution of a nitrile-specifier protein that detoxifies the glucosinolate defenses of their diverse Brassicales hosts. In this Special Feature, Winkler et al. (92), in a new phylogenetic analysis, provide evidence that evolutionary shifts to chemically different plant clades are associated with elevated diversification in leaf-mining flies.

In contrast to the “bitrophic” view on diversification proposed by Ehrlich and Raven (4), Singer and Stireman (93) have recently advocated a “tritrophic niche concept.” In its simplest form, the idea is that factors allowing herbivores to escape predation represent additional niche axes of a species (in combination with adaptations to host plant defenses). Consequently, adaptive divergence and speciation in herbivores might be facilitated by escape from their own enemies and host plant characteristics. Although the escape of herbivores from predation and parasitism is clearly important for insect community structure and host shifts (reviewed in ref. 93), far less attention has been paid to its impacts on diversification. Singer and Stireman suggest that diversification will be promoted when divergent selection imposed by enemies of herbivores is strong (i.e., where attack rates are high), and where ecological opportunity in tritrophic niche space is particularly high (i.e., where competition is low). Their hypothesis could be tested by comparing diversification rates of insect herbivore lineages with different feeding strategies, which apparently show differential rates of enemy attack and competition (93). Additionally, the impact of adaptations to enemies (antipredator behaviors, sequestration of plant toxins, etc.) on diversification rates is essentially unexplored.

Coevolution

As we have noted, “coevolution” has several meanings (94). They include population-level processes of reciprocal adaptation of interacting species, which may be relatively specific or pairwise (two species, each adapting to a characteristic of the other) or more diffuse (multispecific), in which a species adapts to the properties of a set of interactors, and so has genetically correlated responses to several species (51, 52). At a macroevolutionary level, diversity in adaptations of plants to herbivores and vice versa could range from ongoing interactions between antagonist lineages, with relatively short time lags between reciprocal evolutionary changes, to the decoupled, sequential bursts of adaptation and diversification portrayed in Ehrlich and Raven’s “escape-and-radiate” scenario (4).

Demonstrating reciprocal adaptation requires information on function and/or selection on relevant characters. Although adaptations of specialized insects to their hosts have been thoroughly documented, adaptations of plants to specific herbivore species have been shown less frequently, partly because there is less information on the target specificity

of individual defense characters. A few examples have been well documented. European populations of *Barbarea vulgaris* (Brassicaceae) are polymorphic for resistance to a major flea beetle herbivore (*Phyllotreta nemorum*), and the beetle similarly shows a simply inherited polymorphism for utilization of *B. vulgaris* (95). Differences in furanocoumarin profiles among populations of human-introduced *Pastinaca sativa* (wild parsnip) are matched with the detoxification (cytochrome P450) profile of associated populations of the specialist webworm *Depressaria pastinacella* (96), and the thickness of the exocarp in fruits of *Camellia japonica* varies clinally in concert with the length of the rostrum of the plant’s sole seed predator, the weevil *Curculio camelliae* (97). The more difficult problem in such cases is to show that variation in both parties is a consequence of their interaction rather than another environmental variable. Ultimately, reciprocal transplants and measures of selection on specific functional traits in both partners would provide convincing evidence.

Whatever the distribution of the adaptations of plants and herbivores to each other may be along the pairwise/diffuse spectrum, their evolution is clearly an ongoing process. Related plants may be chemically similar, but they nonetheless differ in the identity and levels of compounds that issue from similar biosynthetic pathways, as is clear from comparing the terpenoids of *Bursera* (98), the cardenolides of *Asclepias* (44, 99), and many other examples. In at least some cases, divergence is driven by selection, as shown by DNA sequence patterns at the methylthioalkylmalate synthase (MAM) locus in the glucosinolate synthesis pathway in crucifers (100). Adaptive variation among the detoxifying capacities of insects has also been documented, for instance in the cytochrome P450’s of *Papilio* butterflies (101). Many questions remain, however, about such variation. For example, do new chemical defenses confer advantage because they are more potent (betokening escalation) or simply because they are new? Do new biochemical adaptations of plant or insect compromise earlier or other adaptations? And finally, what is the relationship between population-level adaptations and macroevolutionary processes?

At the macroevolutionary level, we have noted that except in special cases [specifically, the seed-predatory agaonid wasp pollinators of *Ficus* (102)], phylogenies of insects seldom match closely those of their host plants. The more common pattern appears to be that of sequential evolution (103, 104): the as-

sociations have arisen by “colonization” from one plant lineage to another, usually related and therefore chemically similar. The radiation of insect clades associated with specific plant clades shows a degree of temporal correspondence. For example, Zwölfer and Herbst (105) suggested, based on fossil and biogeographic evidence, that the weevil genus *Larinus* is as old (Oligocene) as the thistle clade with which it is associated, and molecular clock estimates suggest that the butterfly subfamily Pierinae arose within ≈ 10 million years of the origin of its hosts (72). How long such clade-level associations, indicative of phylogenetic conservatism, persist is uncertain. Some higher taxa of insects are largely or entirely associated with plant clades that date from the mid or early Tertiary, and others associate with conifers or monocots, which originated in the Early Cretaceous or before. It is not certain that all of the insect clades thus restricted are comparable in age to their host lineages, nor that there exists a continuous age distribution of associations. The strength of any such association will appear to decay with time as lineages of the insect clade colonize and proliferate on other plant clades, as insect lineages on the ancestral plant clade become extinct, and as plant lineages have escaped from some of their erstwhile herbivores by evolving new defenses, a point on which, as we noted earlier, there is little evidence. It may prove possible to glimpse some of these dynamics from sufficiently detailed phylogenies of both insects and plants.

Consequences of Macroevolution for Ecological Communities

There is a growing appreciation among ecologists that long-term evolutionary history has a major role in explaining the composition and structure of ecological assemblages or communities, and phylogenetic approaches are indispensable in achieving explanation (23, 24, 106, 125). The diversity of herbivores associated with plant species in a community [part of what Root (107) termed a “component community”] is not solely a consequence of adaptation of insects to that plant in that region, but is affected by the accessibility of that plant and its relatives, in both the focal region and elsewhere, to lineages of insect herbivores whose diet has been shaped by a very long history, and by genetic constraints that contribute to phylogenetic conservatism. For reasons that are still almost entirely unexplored, but presumably include constraints on genetic variation, some insect clades seem entirely barred from feeding on some plant clades. For instance, almost no butter-

flies feed on the very large family Rubiaceae (108), and the Orchidaceae, one of the two largest plant families, is relatively devoid of associated insect herbivores. Thus the distribution of herbivore diversity, and presumably the impact of herbivory, across plant taxa may be highly imbalanced, in part for historical reasons.

Community ecology cannot be divorced from historical biogeography. A regional flora has been assembled over time by invasion from other areas, perhaps followed by within-region diversification, and the composition of the herbivore fauna, dominated by insects with phylogenetically conservative diets, will likewise have a historical explanation. For example, Futuyma and Mitter (109) analyzed the 90 genera of leaf beetles (Chrysomelidae) recorded from New York. Excluding those with very polyphagous species or poorly recorded diets, 56 genera occur also in a distinct biogeographic region (western North America, tropical America, or Europe). In almost all of the genera, species in New York feed on at least one plant family that is also used as a host by congeneric species in a different region. This pattern was highly nonrandom, and equally strong among genera shared with all three biogeographic regions. Whether a genus spread to New York from elsewhere or vice versa, it is clear that dispersing insect species retain their ancestral host preferences and presumably are integrated into a regional biota or not, depending on the plant species they encounter.

Not surprisingly, then, the structure of the food web, of the plant/herbivore interface, has a strong phylogenetic signal. In a crude effort that preceded the development of molecular phylogenies, Futuyma and Gould (110), using phenetic analysis, found that the similarity of insect communities on tree species in a deciduous forest was somewhat correlated with the plants' taxonomic relationship. Weiblen et al. (111) reported on a massive study in which associations of 524 species of herbivores that were recorded from more than 62 plant species in a New Guinea rain forest were analyzed with reference to plant phylogeny. The faunal similarity of pairs of plants was negatively correlated with their phylogenetic distance, measured by molecular branch length. This correlation explained an astonishingly high 25% of the variance in faunal similarity. In a similar analysis, Ødegaard et al. (112) explained an even higher proportion (35%) of the variance in faunal similarity of beetles on Panamanian plant species by phylogenetic distance.

Ecological and microevolutionary patterns indicate that when closely related plants coexist shared herbivores may impose important impacts on community structure and selection for defensive strategies (113, 114). It is also to be expected, then, that as plant communities assemble over evolutionary time, herbivore impacts may impose selection on divergence among closely related plant species. Becerra (115) recently tested this hypothesis by assessing the chemical similarity of coexisting and noncoexisting *Bursera* spp. from the Mexican dry forest, trees that are attacked by a clade of specialist leaf beetles in the genus *Blepharida*. The pattern that emerges from this analysis is that as the spatial scale of communities decreases (from regional to local), and as the plant-herbivore relationships become increasing tight (i.e., toward monophagy) coexisting *Bursera* tend to be more chemically dissimilar than would be expected by chance. Kursar et al. (35) report a similar pattern in the genus *Inga* in their contribution to this Special Feature. Although it is difficult to determine whether this pattern arose from herbivore-mediated divergent selection or an ecological filter preventing the local establishment of chemically similar species, these studies make explicit the links between phylogeny, defense variation, and the assembly of plant communities.

Similarly, when a plant is first introduced to a region by human transport, it will be colonized soonest by polyphagous herbivores and specialists that are adapted to closely related or chemically similar plants. The fauna of introduced plants, including "invasive" species, largely supports this conjecture (116, 117). A contribution to this Special Feature by Pearse and Hipp (118) takes analyses of the insect communities on nonnative plants to the next level by examining the relative importance of phylogenetic distance (from native species) and specific plant traits for the abundance of insects on North American oaks. In the same vein, introduced specialist insects, if they persist in a new community, generally attack native plants related to their normal hosts (119, 120). For this reason, herbivores that are candidates for biological control are screened for their responses to commercially important plants that are related to the herbivore's natural hosts, and sometimes (too rarely?) are tested on related native wild plants as well.

The phylogenetic, or "deep historical," perspective is a relatively recent addition to an old question: what determines variation among plant species in the diversity of their herbivore fauna?

Such factors as breadth of geographic range, abundance, and structural architecture have been implicated by ecological studies (68, 121). A plant's fauna has doubtless accreted over the course of time: some species of insects will accompany its origin or its spread to a new region, some will use it on first encounter or will adapt to it soon thereafter; others will colonize and adapt to it later, perhaps depending on chemical or phylogenetic propinquity to their normal hosts. Just as it is possible, in principle, to determine the historical sequence in which lineages have invaded and diversified in a regional biota (122–124), so we can envision the possibility of phylogenetically tracing the history of the biota's component communities: the assemblages of animals associated with species of plants. Of course, the phylogenetic history of insect herbivores themselves may contribute to community patterns. In a coevolutionary perspective, both the history and traits of both plant and insect lineages have contributed to their joint diversification and current associations.

Speculation and Future Directions

Here, we outline four major conclusions based on the current trends in the literature and speculate on future directions.

- Current investigations confirm phylogenetic patterns in plant defense and insect host use. Evidence of adaptation is often detected by departures from phylogenetically correlated similarity, such as patterns of convergence. Exceptional shifts in defensive strategy and insect host use will likely be extremely informative, especially if studied in a phylogenetic context involving replicated divergences.
- Plant and insect traits cannot be treated as unitary. Some traits may form coadapted strategies (e.g., sequestration of plant toxins and aposematic coloration in specialist herbivores). Thus, although tradeoffs clearly must constrain evolution, tradeoffs may be difficult to detect between two arbitrarily selected traits and they likely occur at the level of the overall strategies used by plants and insects. The prevalence of such patterns and their effects on trait coevolution are poorly known, although we have a few examples of incremental and directional change during diversification, the consecutive addition of novel strategies, and the replacement of old strategies by new ones.
- Phylogenetic methods to assess the role of traits in diversification range from elegant sister clade compari-

sons to computationally intensive estimates of how traits correlate with speciation and extinction rates. These methods need further elaboration, and their application to plant and insect diversification is in its infancy. Little is known about the role of plant and herbivore traits in diversification, much less their role in coevolution.

- Knowledge of phylogenetic history is proving to be critical in understanding

community interactions. Conversely, community–ecological complexity affects all aspects of the macroevolution of plants and insects. Whether we consider the impact of which plant species coexist in a community, the intensity of predation and parasitism of herbivores, or the extent of specificity of plant defense traits on diverse insects, we can expect community interactions to modify classic coevolutionary predictions. The evolutionary

effects of ecological complexity are little explored and difficult to untangle, yet are surely important.

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